Ecological Applications, 18(6), 2008, pp. 1325–1330

ARE SHRUBLAND BIRDS EDGE SPECIALISTS?

Scott Schlossberg[1,3] and David I. King[2]

[1]*Department of Natural Resources Conservation, University of Massachusetts, 201 Holdsworth Hall, Amherst, Massachusetts 01003 USA*
[2]*Northern Research Station, USDA Forest Service, 201 Holdsworth Hall, University of Massachusetts, Amherst, Massachusetts 01003 USA*

Abstract. In studies of forest fragmentation, birds of scrubby, early-successional habitats are considered edge specialists. Because these birds are assumed to thrive in fragmented, edge-dominated areas, their landscape ecology has received little attention from ecologists. With populations of shrubland birds declining throughout the eastern United States, the question of whether or not these birds really prefer edge habitats has important conservation implications. We used a meta-analysis to test how edges affect the abundance of shrubland birds in early-successional habitats. We analyzed data for 17 species from seven studies that compared the abundances of birds in the interiors and edges of regenerating clearcuts surrounded by mature forest. The meta-analysis clearly showed that shrubland birds avoid edges. All 17 species tested had higher abundances in patch centers than along edges, and edge effects were significant for 8 of 17 species. The key implication of this result is that small or irregular patches, dominated by edge, are unlikely to provide suitable habitat for shrubland birds. Thus, management for these declining species should involve providing large patches and minimizing edges. These findings demonstrate the importance of testing widely accepted ecological classifications and the need to view landscape ecology from the perspective of non-forest wildlife.

Key words: clearcut; early-successional; ecotone; edge avoidance; edge effects; fragmentation; meta-analysis; shrubland birds.

Introduction

Much of our understanding of landscape ecology comes from research on forest fragmentation (e.g., Wilcove 1985, Bierregaard et al. 1992, Andren 1994, Robinson et al. 1995). A large body of research, for instance, has demonstrated that forest edges are poor habitats for songbirds (Gates and Gysel 1978, Brittingham and Temple 1983, Morse and Robinson 1999, Flaspohler et al. 2001). Microclimates near edges are more extreme than in habitat interiors (Saunders et al. 1991), and, in fragmented or agricultural landscapes, predators can be more abundant along edges than in forest interiors (Chalfoun et al. 2002). Birds nesting near forest edges often suffer from decreased nest success (Batary and Baldi 2004). For all of these reasons, some birds appear to avoid edges and small patches that are dominated by edge (Parker et al. 2005, Lindell et al. 2007).

From this forest-fragmentation perspective, birds of scrubby, early-successional habitats are "edge species" because they primarily occur along forest edges or in small woodlots (e.g., Whitcomb et al. 1981, Freemark and Collins 1992). As a result, one might expect these birds to be insensitive to or even benefit from habitat fragmentation (Boulinier et al. 2001). The problem with this inference is that much research on forest fragmentation has taken place in landscapes consisting solely of mature forest and agricultural fields or residential areas. In such landscapes, the edges of woodlots may be the only areas with the dense vegetation preferred by shrubland birds (Imbeau et al. 2003). Thus, use of forest–field edges does necessarily indicate a general affinity for ecotones or insensitivity to fragmentation. Moreover, forest edges are marginal habitats for shrubland birds, many of which are more abundant in early-successional habitats such as old fields or regenerating forests (Fink et al. 2006). Because shrubland birds have been considered edge species, their responses to edges and fragmentation in shrublands have been largely neglected (Rudnicky and Hunter 1993). Only in the last few years have researchers begun to explore how

Manuscript received 4 January 2008; revised 3 March 2008; accepted 7 March 2008. Corresponding Editor: R. L. Knight.
[3] E-mail: srs@nrc.umass.edu

fragmentation of shrubland habitats affects shrubland birds (Krementz and Christie 2000, Rodewald and Vitz 2005, Askins et al. 2007).

Shrubland birds are declining throughout the eastern United States (Askins 1993, Brawn et al. 2001), as shrubland habitats disappear and become increasingly fragmented (Askins 2000, Trani et al. 2001, Brooks 2003). Thus, understanding how shrubland birds respond to edges in early-successional habitats has important implications for conservation of this bird community. Forests regenerating after logging are the largest source of habitat for shrubland birds in the East; however, logging practices have been changing recently. Historically, logging involved large clearcuts, but public opposition to clearcutting is causing it to be replaced by small group-selection cuts in many areas (Askins 1994, 2001, Rodewald and Vitz 2005). If shrubland birds are averse to edges, then larger patches may be necessary to conserve these species. On the other hand, if shrubland birds actually do prefer edges, then fragmentation of shrublands may not be a conservation problem. To address this knowledge gap, we conducted a meta-analysis of studies examining how shrubland birds respond to edges in early-successional habitats.

Methods

Our study focused on birds that regularly breed in early-successional woody habitats in the eastern United States. We developed a list of such species based on a quantitative review of habitat usage studies (S. Schlossberg and D. I. King, *unpublished manuscript*) and published accounts of avian habitat preferences (American Ornithologists' Union 1998, DeGraaf and Yamasaki 2001). To be included in the meta-analysis, a study had to report avian abundances in the interior of shrubland patches and along edges adjacent to mature forest. We used forest as the adjacent habitat because forests are the natural vegetation type in most of the eastern United States. We searched for publications, including theses, using the online databases *Biological Abstracts* and *ISI Web of Knowledge* and the reference sections of publications. Studies could take place in any type of shrubland in the eastern United States, though all studies we used took place in clearcuts less than eight years old. To avoid confounding edge effects with area sensitivity, we only included studies in which the scrub–shrub patches sampled were at least 1 ha in size. This is above the threshold for area sensitivity for most shrubland birds (Kerpez 1994, Annand and Thompson 1997, Costello et al. 2000). We excluded studies conducted in utility rights-of-way because birds may respond differently to edges in long, linear strips than in discrete patches.

From each study we extracted the abundance or density of each bird species in interior and edge habitats. All edge samples were taken within 30 m of the forest–shrubland boundary, and interior points were located >60 m from the boundary; we did not use data collected between 30 m and 60 m from the forest edge. For studies reporting results for separate years or study sites, we averaged results for each species for interior and edge sites. To ensure adequate sample sizes, we analyzed data only for species that occurred in two different studies and for which we had at least six data points. Our response variable for the meta-analysis (the effect size) was the standardized difference between each species' abundance in the patch interior and along the edge. For each species in each study, this was computed as $(d_i - d_e)/s$, where d_i is the bird's density (or abundance) in the interior, d_e is the density in the edge, and s is the pooled standard deviation (Lipsey and Wilson 2001). This is the difference between interior and edge habitats relative to the variation among replicates. Effect sizes greater than 0 indicate edge avoidance while negative effect sizes indicate attraction to edges.

Three studies included in the meta-analysis did not provide standard errors of density or abundance estimates (DeGraaf 1992, Kerpez 1994, Talbott and Yahner 2003). To estimate effect sizes for these studies, we had to estimate their standard errors. Because the data were counts of birds, we assumed the counts would have a Poisson distribution. We, therefore, used the Poisson estimate for the standard deviation (the mean) to estimate standard errors. We consider this a conservative estimate of precision because the mean coefficient of variation (CV) for the studies that included standard errors was 69% (vs. 100% for the Poisson estimate). Results were robust to the CV estimate we used. Even if we assumed a CV that was twice as high as the reported level (138%) for studies failing to report error levels, results were still significant for seven of the eight species with significant edge effects at a CV of 100%.

Based on a nonsignificant test for heterogeneity of effect sizes, we used a fixed-effects model to compute the mean effect size for each study and species (Lipsey and Wilson 2001). One complication was that the studies in the meta-analysis differed in how they sampled edge habitats. For three studies, the edge was the strip of clearcut adjacent to the surrounding forest, and all of the bird counts were conducted entirely within early-successional habitat. In the other four studies, edge samples were centered at the forest–clearcut boundary, so edge plots included some forest. If shrubland birds do not use forests, sampling into forests could result in lower bird counts and potentially inflate edge effects. To determine whether or not the edge sampling method influenced our results, we compared mean effect sizes for the two methods using a two-group z test.

Results

Seven studies met our criteria for inclusion in the meta-analysis, and we were able to estimate effect sizes for 17 bird species (Table 1). Overall, birds avoided edges (mean effect size $\pm$ SE = 0.56 $\pm$ 0.01). All 17 species had positive effect sizes, and eight species' effect sizes were significantly greater than zero (Table 2).

TABLE 1. Studies used in a meta-analysis of edge effects on the abundance of shrubland birds.

Study	Study location	No. study sites†	Effect size‡ (mean ± SE)
DeGraaf (1992)	New Hampshire	8	0.50 ± 0.20
Fink et al. (2006)	Missouri	6	0.57 ± 0.30
Rodewald and Vitz (2005)	Ohio	24	0.56 ± 0.15
Talbott and Yahner (2003)	Pennsylvania	20	0.70 ± 0.13
Yahner (1987)	Pennsylvania	6	0.04 ± 0.26
Elliott (1987)	Maine	8	0.50 ± 0.25
Kerpez (1994)	Virginia	8	0.68 ± 0.31

† Including both edge and interior sites.
‡ Effect size is the difference in abundance between patch edge and center, scaled by within-study standard deviation.

When analyzed by study, birds in five of the seven studies showed significant avoidance of edges, and one other study had a significance level of 0.06 (Table 1). When the studies were divided based on whether or not edge plots extended into adjacent forests, studies that sampled into forests ($\bar{X} = 0.41 \pm 0.09$) and studies that sampled only in clearcuts ($\bar{X} = 0.65 \pm 0.12$) both showed significant edge avoidance. Edge avoidance was stronger in studies where edge samples were entirely within the clearcuts ($z = 2.86$, $P = 0.01$).

DISCUSSION

In our meta-analysis, all 17 species of shrubland bird were more abundant in the interiors of clearcuts than along edges, with results significant for eight species. Each of these eight species has previously been labeled an "edge species" in studies of forest fragmentation (Whitcomb et al. 1981, Freemark and Collins 1992). Some, such as Indigo Bunting, Field Sparrow, and Yellow-breasted Chat, have actually been termed "edge specialists" (Hansen and Urban 1992, Villard 1998). The results of our meta-analysis suggest that most shrubland birds are actually averse to forest–shrubland edges in shrubland habitats. Even the birds that did not show significant edge avoidance were, at best, neutral toward edges. This suggests that usage of forest edges by shrubland birds in forest-fragmentation studies was due to lack of suitable habitat rather than a preference for edges (Imbeau et al. 2003).

We expected effect sizes to be greater in studies that sampled into forests than in studies sampling only in clearcuts. In actuality, effect sizes were higher in studies conducted only in clearcuts than in studies extending into forests. This difference, however, is almost entirely due to the small effect size for the study by Yahner (1987). His study was unique in that it had only three study sites, and they varied widely in age and forest type. The result was high variation in avian abundances among replicates and correspondingly low effect sizes. After removing Yahner's study from the meta-analysis, we found no significant difference in the effect sizes for the two sampling methods ($z = 1.34$, $P = 0.33$). This suggests that the edges of shrubland habitats and the surrounding forests are both avoided by shrubland birds in roughly equal measure. Core scrub–shrub habitats are clearly the most preferred habitat for these birds.

Excluding Yahner (1987), the remaining six studies in our meta-analysis differed in methodology as well as in the age and structure of the early-successional habitat. Still, when analyzed by study, all six studies had similar

TABLE 2. Results from a meta-analysis of edge effects on abundances of shrubland birds.

Species	Mean effect size†	95% confidence interval	P‡	No. studies
Ruffed Grouse (*Bonasa umbellus*)	0.86	0.06–1.66	0.04	2
White-eyed Vireo (*Colinus virginianus*)	0.04	−0.67–0.76	0.90	2
Gray Catbird (*Dumetella carolinensis*)	0.53	−0.26–1.31	0.19	2
Cedar Waxwing (*Bombycilla cedrorum*)	0.99	0.28–1.71	0.01	3
Blue-winged Warbler (*Vermivora pinus*)	0.82	0.07–1.56	0.03	2
Nashville Warbler (*Vermivora ruficapilla*)	0.33	−0.57–1.23	0.48	3
Chestnut-sided Warbler (*Dendroica pensylvanica)*	0.43	−0.20–1.06	0.18	4
Prairie Warbler (*Dendroica discolor*)	0.55	0.02–1.07	0.04	4
Black-and-white Warbler (*Mniotilta varia*)	0.18	−0.39–0.76	0.53	5
Common Yellowthroat (*Geothlypis trichas*)	0.37	−0.12–0.85	0.14	5
Yellow-breasted Chat (*Icteria virens*)	0.96	0.37–1.55	0.001	3
Eastern Towhee (*Pipilo erythrophthalmus*)	0.37	−0.13–0.86	0.15	5
Field Sparrow (*Spizella pusilla*)	1.02	0.49–1.55	<0.001	5
White-throated Sparrow (*Zonotrichia albicollis*)	0.47	−0.53–1.47	0.35	2
Dark-eyed Junco (*Junco hyemalis*)	0.81	−0.28–1.90	0.15	2
Indigo Bunting (*Passerina cyanea*)	0.69	0.17–1.20	0.01	5
American Goldfinch (*Carduelis tristis*)	0.95	0.28–1.62	0.01	4

† Effect size is the difference in abundance between patch edge and center, scaled by within-study standard deviation.
‡ Based on a z test.

effect sizes, with each study showing evidence of edge avoidance (Table 1). In contrast, one study that could not be included in our meta-analysis reported no evidence of edge avoidance for birds in Maine clearcuts (Rudnicky and Hunter 1993). In that study, however, distance to edge was measured as a proportion of the patch radius rather than as the actual distance to the edge. This methodology could have obscured birds' actual responses to edges. Thus, we conclude that edge avoidance by shrubland birds is a general phenomenon in regenerating forests of the Northeast.

Why most shrubland birds avoided edges was not revealed by the studies that we reviewed. Research in forests has shown that habitat quality, as determined by vegetation structure or food availability, often differs between the interiors and edges of woodlots (Burke and Nol 1998, Zanette et al. 2000, Van Wilgenburg et al. 2001). Two studies investigating arthropod abundance in clearcuts reported no difference between patch centers and edges (Shure and Phillips 1991, Rodewald and Vitz 2005). The latter study also reported no effect of proximity to edge on fruit availability. Research has shown that microclimate changes predictably as one moves from the edge to the center of a clearcut, the latter being sunnier, drier, and warmer than the edge (Godefroid et al. 2006). As a result, plant species composition and vegetation structure can differ between edges and centers of clearcuts (Minckler and Woerheide 1965, cf. Rodewald and Vitz 2005). Whether shrubland birds are responding to edge-related changes in vegetation or climate needs further investigation. Another possible explanation for edge avoidance is that restrictions on territory placement near edges cause passive displacement of bird territories away from ecotones (King et al. 1997). In future studies, this hypothesis could be tested by comparing observed territory locations with simulations of random territory placement.

Nest predation is another common explanation for edge avoidance in birds, but evidence suggests that shrubland birds are not responding to heightened predation near edges. King et al. (1998) did find that three types of predators were slightly more abundant along the edges of clearcuts than in patch centers. Shrubland birds can, however, nest successfully along edges or in edge-dominated areas like group-selection cuts or utility rights-of-way (Woodward et al. 2001, King and Byers 2002, King and DeGraaf 2004, Chandler 2006). At present, there does not appear to be a general tendency for predators to be especially abundant or problematic at the edges of shrubland habitats. In contrast, nest predation in forests is frequently greater along edges than in forest interiors (Batary and Baldi 2004). This shows, again, that applying results from studies of forest fragmentation to shrubland birds can be misleading.

Edge avoidance may contribute to area sensitivity in shrubby habitats. Forest openings, such as group-selection cuts or managed wildlife areas, are often smaller than 1 ha and are essentially all edge, with no core habitat. Several studies have reported that shrubland birds are less abundant in these small openings than in larger clearcuts, as would be expected for birds that avoid edges (Kerpez 1994, Annand and Thompson 1997, Costello et al. 2000). As further evidence for the relationship between edge and area sensitivity, three shrubland birds that regularly breed in small forest openings (Black-and-white Warbler, White-eyed Vireo, and Eastern Towhee) had some of the lowest effect sizes in our meta-analysis (S. Schlossberg and D. I. King, *unpublished manuscript*). Interestingly, all three of these species will sometimes nest in the understory of mature forests (S. Schlossberg and D. I. King, *unpublished manuscript*). In contrast, species that rarely use mature forests, such as Blue-winged Warbler and Field Sparrow, showed greater avoidance of edges. This suggests that for many shrubland species, edge avoidance is related to a general avoidance of tall trees or mature forests.

If shrubland birds are not edge species, then what exactly is an edge species, and do such species exist? Imbeau et al. (2003) suggested that merely inhabiting an ecotone does not define an edge species. Rather, an edge species must make use of both of the adjacent habitats (see also Ries et al. 2004). By this definition, few birds included in our meta-analysis would actually be considered edge species. One exception may be Indigo Buntings, which nest in scrubby areas, but appear to prefer territories with tall trees, used as song posts (Taber and Johnston 1968). Still, buntings were edge adverse in our meta-analysis, suggesting that their usage of edges and tall trees may be opportunistic rather than obligate. In a study of forest–heath ecotones in Australia, Baker et al. (2002) found that many bird species used the ecotones, but those birds could also be classified as preferring forests or heaths. His results, along with ours, suggest that few or no birds may be true ecotone specialists.

The obvious management implication of our meta-analysis is that shrubland birds will benefit from decreasing fragmentation of early-successional habitats. Managers interested in aiding shrubland birds should provide large habitat patches, avoid irregular patch shapes and edges, and minimize interspersion of openings and mature forests. Logging is the most cost-effective means to provide habitat for shrubland birds. Contrary to popular opinion about logging, applying the above management prescriptions could actually benefit forest-interior songbirds. For a given total area to be logged, a few large clearcuts will create less edge than many small group-selection openings (Thompson 1993). Moreover, clearcuts and other silvicultural treatments are temporary and will succeed to mature forests within a few decades. Given these considerations, we suggest that managers need to reconsider recent efforts to minimize the size of logged openings and consider using larger clearcuts in appropriate locations.

Another important implication of our findings is the importance of considering avian patch and landscape ecology from perspectives besides forest fragmentation. Forests are not the only habitats that have edges, and our meta-analysis shows that shrubland birds have their own large-scale habitat preferences that may be important for conservation. Early findings that shrubland birds prefer edges made it easy to dismiss the landscape ecology of this bird community (see Rudnicky and Hunter 1993). This shows the dangers of making ecological classifications based on limited evidence (Villard 1998). For the future, we hope that ecologists recognize that the conservation of shrubland birds will depend on how these birds respond to the patch and landscape features of shrubland habitats.

Acknowledgments

Thanks to the Natural Resources Conservation Service for supporting S. Schlossberg and our review of the ecology of shrubland birds. Two anonymous reviewers provided comments that helped us to improve the manuscript greatly.

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